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THE UNIVERSITY OF ALBERTA

Some Aspects of the Population Biology and Physiological Ecology of *Aralia nudicaulis* L.

by

Lawrence B. Flanagan

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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FACULTY OF GRADUATE STUDIES AND RESEARCH

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Walter Moser
Supervisor

Date Nov. 9, 1984

Abstract

This study used demographic and physiological methods to study various characteristics affecting survival and reproduction in *Aralia nudicaulis*.

The pattern of ^{14}C assimilate distribution was studied to determine the extent of physiological integration among individual shoots in a clone. The experiments showed that most of the carbon assimilated by a shoot remained within that shoot after 24 hours. Most of the carbon exported by a shoot was translocated basipetally into the rhizome section adjacent to the shoot. While the rhizome basipetal to a shoot was a major storage organ, the roots and new rhizomes adjacent to a shoot had the highest specific activity.

Changes in the normal pattern of translocation were observed when one shoot was shaded before an adjacent shoot was labelled. Plant components normally supplied with carbohydrate from the shaded shoot were supplied with carbohydrate from the labelled shoot. The changes in pattern of translocation after disturbance indicated the integrated nature of shoots within a clone.

Experiments were conducted to test the effect of gibberellic acid and light quality on flower bud initiation. Flowering in 1984 was not affected by 1983 applications of GA, or CCC, an inhibitor of GA biosynthesis, to flowering shoots. In addition, flowering was not affected by two shade treatments: (1) reduced light intensity, and (2) reduced light intensity and reduced Red:Far-Red ratio. None of the

experimental treatments altered the flowering pattern of treated shoots from that observed for untreated shoots. Flowering in consecutive years seemed to be affected by the cost of reproduction. Of the untreated shoots only 4.8% of females compared to 35.1% of males flowered in consecutive seasons.

Aralia nudicaulis is sexually dimorphic for a number of characteristics including inflorescence size and flowering phenology. Females had fewer flowers per inflorescence and some flowered earlier in the season than males. Individual females that flowered early in the season had fewer flowers than females that flowered later in the season. The effects of variation in flower number and phenology on pollination and seed set were studied to determine the adaptive significance of these characteristics.

Flowering time was significantly correlated with seed production in 1983 and 1984, but the relationship differed between the two years. Seed production was highest at peak flowering in 1983 and was highest in the later stages of flowering in 1984. There was a significant positive correlation between flower number and total seed production and seed set per flower in 1983 and 1984. However, in both years the significance of this relationship varied within the flowering season. Pollination was required for seed set to occur because there was no apomictic seed production. There was no evidence for pollen limitation of seed set in 1983, but pollination intensity limited seed set per flower

on two dates in 1984. It was not possible to conclude that a particular characteristic was adaptive because of the variation in selection and the interaction of several characteristics affecting seed production.

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Table of Contents

Chapter — Page

1. Introduction 1

2. Pattern of ^{14}C assimilate distribution 9

2.1 Introduction 9

2.2 Materials and Methods 11

2.2.1 Growth habit of *Aralia nudicaulis* 11

2.2.2 Experiment 1 13

2.2.3 Experiment 2 13

2.3 Results 15

2.4 Discussion 23

3. Effect of gibberellic acid and light quality on flowering 27

3.1 Introduction 27

3.2 Materials and Methods 29

3.2.1 GA_4 and CCC application 33

3.2.2 Shading experiments 33

3.3 Results 36

3.3.1 Size of flowering and non-flowering shoots 36

3.3.2 Consecutive flowering pattern of untreated flowering shoots 40

3.3.3 Effect of GA_4 and CCC on flowering 40

3.3.4 Effect of shading on flowering 42

3.3.5 Effect of $GA_{4,7}$, CCC and shading on shoot size 45

3.4 Discussion 52

4. Intrapopulation variation in secondary sex characteristics 56

4.1 Introduction 56

4.2 Materials and Methods 58

4.3 Results 62

4.3.1 Inflorescence size 62

4.3.2 Flowering phenology 65

4.3.3 Relations of flowering phenology and pollination intensity with seed set 71

4.3.4 Correlation of ramet size with seed set ...72

4.3.5 Correlation of inflorescence size with seed set 73

4.3.6 Relationship between spatial pattern and seed set 73

4.4 Discussion 82

5. Integration 87

6. Literature Cited 92

7. Appendix 105

7.1 Dry weight of plant components 105

List of Tables

Table — Page

1. Specific activity of the component plant parts in a three-shoot plant system.....18

2. Change in specific activity when shade is applied to S2 in a two-shoot system.....21

3. Change in specific activity when shade is applied to S1 in a two-shoot system.....22

4. Mean values for the leaf characteristics of flowering and non-flowering shoots.....37

5. Demographic behavior of flowering ramets.....41

6. Effect of GA_4 and CCC on flowering in male and female shoots.....43

7. Effect of shade treatments on flowering in male and female shoots.....44

8. Two-way ANOVA of the effect of sex and growth substance on the % change in performance index....46

9. Effect of growth substances on % change in performance index.....47

10. Two-way ANOVA of the effect of sex and growth substance on the % change in petiole length.....48

11. Effect of growth substances on the % change in petiole length.....49

12. Effect of shading on % change in petiole length.....50

13. Effect of shading on % change in performance index.....51

14. Frequency of umbel number.....64

15. Flower number, seed production and mean seed weight in 1983.....66

16. Flower number, seed production and mean seed weight in 1984.....67

17. Mean size characteristics of female ramets that reached full bloom on different dates.....74

18. Summary of linear regressions relating shoot size to seed set per flower.....75

19. Summary of linear regressions relating shoot size to number of flowers per inflorescence.....76

20. Summary of linear regressions relating flower number to total seed production in 1983.....77

21. Summary of linear regressions relating flower number to seed set per flower in 1983.....78

22. Summary of linear regressions relating flower number to total seed production in 1984.....79

23. Summary of linear regressions relating flower number to seed set per flower in 1984.....80

24. Summary of linear regressions relating distance to the nearest male flowering ramet to seed set per flower.....81

List of Figures

Figure — Page

1. Diagrammatic representation of a three-shoot plant system.....14

2. The pattern of ^{14}C assimilate distribution in a three-shoot plant system.....17

3. The distribution pattern of ^{14}C assimilates exported by shoot 1 of a two-shoot plant system under control conditions and when shade has been applied to shoot 2.....19

4. The distribution pattern of ^{14}C assimilates exported by shoot 2 of a two-shoot plant system under control conditions and when shade has been applied to shoot 1.....20

5. The spectral photon distribution of full sunlight and light penetrating the forest canopy of the study site.....30

6. The relationship between performance index and leaf area.....32

7. The spectral photon distribution of light transmitted through the experimental light filters.....35

8. Frequency distribution of performance index in flowering and non-flowering ramets.....38

9. Frequency distribution of petiole length in flowering and non-flowering ramets.....39

10. Frequency distribution of flower number in female and male inflorescences.....63

11. Cumulative flowering curves for female and male ramets in 1983.....68

12. Cumulative flowering curves for female and male ramets in 1984.....69

13. Flowering curves for female and male flowers in 1983.....70

1. Introduction

Population biology is the study of changes in the number of organisms in a defined area (Harper 1977, p. 1). The way a population changes depends on the structure or secondary characteristics of its component members. Factors such as the age distribution, size distribution and sex ratio of a population will affect one or all of the four demographic processes by which population change occurs: births, deaths, immigration and emigration (Harper 1977, p. 1). Change is also influenced by organisms interacting with their biotic and abiotic environment. Therefore a population biologist seeks to determine how population structure, the environment and demographic processes interact to change population size (Harper 1977, p. 1).

Plant population biology is studied at two levels of organization. Plants can be considered a population of parts because of their modular organization whereby a single structural unit is reiterated during development (Harper and Bell 1979). The growth of plants is a demographic process marked by the birth and death of component parts. Demographic methods may be applied to the change in number of parts as well as the change in the number of individual plants in a population (Bazzaz and Harper 1977). In some plants, modular growth continues for only a short time and is ended by seed production. The demography of individual plants is the dominant level of population study in these plants (Harper 1980). In other plants, the establishment of

new individuals is rare, but individuals have very long lifespans. Plant growth is the dominant population process in these plants (Harper 1980).

While a population is described by its group characteristics, statistical measures that can't be applied to individuals, it is the variation among individuals within populations that is important. Individual variation is what allows change to occur through differential survival or reproduction or both. Survival and reproductive success are combined to determine relative evolutionary fitness. Darwin (1859) recognized variation among individuals as the most essential property of natural populations. He saw evolution as the conversion of this variation among individuals to variation among populations and finally to variation among species.

Evolutionary biologists are most interested in the variation among individual plants and therefore are generally not interested in the demography of plant parts. However, important variation can also occur within a plant. Plant modules can vary in morphological expression and may also vary genetically due to somatic mutation (White 1984). The ecological and evolutionary implications of genetically distinct modules within a plant are still poorly understood (White 1984). Several recent studies have suggested that this variation is important in plant herbivore interactions (Whitham and Slobodchikoff 1981, Gill and Halverson 1984).

Evolutionary changes can occur in a population if three conditions are met: (1) phenotypic variation exists in a population; (2) the variation has a heritable genetic component; and (3) selection acts on the variation (Silvertown 1982). Where it is possible to analyze the demography of different phenotypes separately, it is also possible to determine which phenotype is the most fit and therefore in what direction selection is acting (Silvertown 1982).

Demographic studies often describe differential survival and reproduction among individuals within populations (Sarukhan et al. 1984). Demography alone does not explain why there is individual variability in survival or reproduction. Explanation of the source of such variability requires the study of physiology and genetics. Recently it has been suggested that population biologists should combine physiological studies with demographic studies (McGraw and Wulff 1983). In particular, it would be useful to determine how differences in physiological characteristics among individuals affect reproduction and survival (Bazzaz 1984, Jefferies 1984, Sarukhan et al. 1984). This would allow a more mechanistic understanding of the selection forces in the environment (Jefferies 1984). "The real influence of the environment surrounding an individual will only be adequately understood when the demographic consequences of different physiological traits on survival, growth and reproduction are known" (Jefferies

1984).

This study uses demographic and physiological methods to study various characteristics affecting survival and reproduction in *Aralia nudicaulis*. Two features of *A. nudicaulis* make it an interesting study organism: (1) it is a large clonal perennial plant, and (2) it is dioecious, unisexual flowers of one sex are born on a single individual.

Recently there has been a good deal of interest in trying to determine the ecological and evolutionary advantages of clonal growth (Cook 1983, White 1984). Harper (1977, p. 27) suggested that plant growth has been dominated by two general selective pressures: (1) to attain height and shade neighbours, and (2) to expand laterally and reach limited water and nutrients. Other advantages to clonal growth besides enhanced capacity to harvest resources have been suggested. Cook (1979) suggested that the selective advantage of the clonal habit in plants could be viewed as spreading the risk of genet extinction among a number of independent ramets. However, in several clonal plants ramets do not readily fragment so that a large system of physically connected shoots occurs. In these plants individual ramets may survive if severed from the clone. The question then becomes, what is the advantage of ramets remaining connected together? Bazzaz (1984) suggested that physically connected and physiologically integrated ramets may respond less sensitively to differential resource limitations imposed by

a variety of biotic and abiotic factors. Physiologically integrated ramets may successfully occupy a poor patch where an independent ramet would not be successful (Bazzaz 1984). Bawa et al. (1982) suggested that the cost of reproduction for an individual ramet would be reduced if the resources for reproduction were shared between physiologically integrated ramets. The first step in determining the significance of clonal growth is to determine the extent of physiological integration among connected ramets. Therefore the first objective of this study was to determine the extent of physiological integration of ramets within a clone of *A. nudicaulis*.

Reproductive success in plants is directly controlled by flowering. In obligate outcrossing species like dioecious plants, reproductive success is also affected by secondary characteristics like the number and spatial distribution of compatible mates in a population (Antonovics and Levin 1980). Flowering is known to be affected by a number of environmental factors. Environmental factors which affect flowering in male and female plants differently, would be of particular interest to study. These environmental factors would not only affect reproductive success directly through flower production but would also have secondary affects by altering the sex ratio.

Recent published observations of the flowering sex ratio in natural populations of *A. nudicaulis* have suggested a possible mechanism controlling flowering in this plant. In

open areas (roadsides) equal numbers of male and female plants have been observed flowering (Barrett and Helenurm 1981). In forested areas, a male biased sex ratio is observed. The critical difference between the two habitats is probably light (Barrett and Helenurm 1981). In a forest understory both light intensity and light quality are changed (Holmes and Smith 1977). The change in light quality, particularly the reduced red:far-red ratio, may affect flowering. In response to red light plants produce gibberellins (Cooke et al. 1975) and gibberellins are known to promote flowering in several plant species (Williams and Morgan 1979). Therefore in the forest understory the reduced red light may not allow for enough gibberellin production for flowering to occur. In dioecious species, females have been observed to have higher endogenous levels of gibberellins when flowering than male flowering plants (Leshem and Ophir 1977). Therefore the change in light quality in the forest understory would particularly affect flowering in females, if they required a higher level of gibberellin production than males for flowering to occur. The second objective of this study was to test the hypothesis that flowering in *A. nudicaulis* is effected by light quality changes mediated through phytochrome-controlled release of gibberellins.

Secondary sex characteristics have been noted for many animal and plant species (Lloyd and Webb 1977, Willson and Burly 1983). Darwin suggested that variations in secondary

sex characteristics are accumulated by natural and sexual selection, "... to fit the two sexes of the same species to each other or to fit the males and females to different habits of life or the males to struggle with other males for the possession of the females" (Darwin 1859). Several people have speculated on the adaptive significance of secondary sex characteristics in plants, but at present there have been few tests of these speculations (Lloyd and Webb 1977, Valdeyron and Lloyd 1979, Bullock and Bawa 1981). The adaptive significance of a characteristic may be determined by analysing the effect that variation in that characteristic has on fitness (Silvertown 1982). However, selection for one characteristic is often accompanied by compensation in some other characteristic (Bradshaw 1984). This correlated response to selection is well known in plants and is often the result of several genes controlling the development of a characteristic (Bradshaw 1984). In order to determine how a group of characteristics may have evolved it is necessary to determine the interaction and tradeoffs among characteristics as well as their effects on fitness.

Aralia nudicaulis has been shown to be sexually dimorphic for several characteristics (Barrett and Helenurm 1981, Bawa et al. 1982). Barrett and Helenurm (1981) have speculated on the adaptive significance of several of these secondary sex characteristics. The third objective of this study was to test some of Barrett and Helenurm's (1981)

speculations by determining the effect that variation in different characteristics has on fitness. In addition, an attempt was made to identify the interactions and tradeoffs among factors affecting the evolution of secondary sex characteristics in *A. nudicaulis*.

2. Pattern of ^{14}C assimilate distribution

2.1 Introduction

Several woodland and forest herbs grow and proliferate by the formation of rhizomes and stolons (Cook 1983). This growth process is possible because of the modular architecture of plants whereby a single structural unit is reiterated during development (Harper and Bell 1979). While the growth pattern of clonal plants may appear complex, it can often be explained by simple and repetitive branching rules (Bell 1984).

In some clonal plants, the connections between shoots or ramets do not fragment so that a large system of physically connected shoots occurs. Demographic studies of such plants have shown that, despite relatively constant ramet population size, there is a great turnover of individual ramets (Sarukhan and Harper 1973, Noble et al. 1979, Lovett-Doust 1981, Newell et al. 1981). Although other interpretations exist (see Noble et al. 1979), Cook (1983) has suggested that such turnover of ramets is similar to the senescence of the lower leaves of a non-clonal plant as nutrients from these leaves are transported to actively growing meristems at the top of the plant. Cook (1983) stated that proper interpretation of the demography of shoots depends on knowledge of the development of a clone as well as knowledge of the extent of physiological integration of shoots within a clone.

Little known about the physiological relationships among individual shoots in clonal forest herbs (Newell 1982). The presence of physical connections between shoots does not necessarily indicate the presence of physiological integration. In a study of two clonal forest herbs that maintain physical connections between shoots, there was evidence of physiological integration in one of the species, *Clintonia borealis* (Ashmun et al. 1982). In the other species, *Aster acuminatus*, connected shoots were physiologically independent.

Aralia nudicaulis L. is an herbaceous, perennial plant commonly found in the understory vegetation in the boreal forest regions of North America. In *A. nudicaulis* large clones are formed by the growth of a subterranean rhizome. The rhizome does not readily fragment so that an extensive system of connected shoots may occur (Edwards 1984). The purpose of this study was to determine the extent of physiological integration of shoots within a clone of *A. nudicaulis*. Specifically the study addresses the following two questions:

(1) What is the pattern of ^{14}C assimilate distribution in a clone?

(2) Does the pattern change when an individual shoot is shaded?

2.2 Materials and Methods

2.2.1 Growth habit of *Aralia nudicaulis*

Aralia nudicaulis is a rhizomatous, perennial herb with a short thick caudex bearing a single compound leaf. Dormant buds are produced along the rhizome axis at approximately 5 cm intervals as the rhizome grows. After a period of growth, the rhizome apex turns erect to become a shoot. This causes a dormant bud a few centimeters behind the apex to grow out to replace the rhizome. Growth of the clone occurs by the repetitive production of shoots and regeneration of rhizome growth (Bawa et al. 1982). Shoots are usually produced at one meter intervals along the rhizome (Edwards 1984), however, this distance may be shorter or longer depending on the growth environment. In addition, dormant buds on rhizome sections between shoots may grow out to result in a proliferative (*sensu* Tomlinson 1974) branching pattern. Growth of dormant buds on rhizome sections between shoots occurs frequently in the nutrient rich conditions plants receive in the greenhouse. This suggests that apical dominance in the rhizome is normally maintained by competition among buds on a rhizome for limited water and nutrients (McIntyre 1971, 1972, 1981).

In early May 1983 and 1984, dormant rhizomes were excavated from areas adjacent to permanent study plots of the University of Alberta Hondo Research Laboratory near Hondo, Alberta. Large sample sizes were impossible to obtain

because of the difficulty of excavating long sections of rhizomes without damaging them. Excavated rhizomes were wrapped in moss and sealed in plastic bags for transportation to Edmonton. Subsequently, the rhizomes were planted in a mixture of peatmoss and vermiculite (1:1) in plant flats and placed in the greenhouse. Soil was kept damp until shoots began to emerge from previously formed buds on the caudex. Plants were then watered alternately with distilled water or full strength Hoagland's nutrient solution every second day. Temperature in the greenhouse was maintained at approximately 22 C.

Plants were labelled in a large fumehood that was illuminated by a quartz-iodine lamp (350 umol m^{-2} sec^{-1} (PAR); 14:10 hrs, light:dark; 25 C). Plants were transferred to the fumehood 24 hours before the label was applied. Four hours after the start of the photoperiod, an individual shoot was sealed in a 30 X 50 cm plastic bag. A 50 ml syringe was attached to the bag via a 20 cm length of catheter tubing. ^{14}C carbon dioxide was released into the bag by mixing 10 ul of $Na_2{}^{14}CO_3$ and 30 ul of 1 N H_2SO_4 in the syringe. Individual shoots were exposed to 25 uCi (.925 MBq) of $^{14}CO_2$ for 20 minutes then allowed to translocate the labelled assimilates for 24 hours.

After labelling, the plant was divided up into its component parts as outlined in Fig. 1, dried at 70 C for 36 hours and weighed. Three samples (50 mg) of each plant part were then combusted in a biological material oxidizer (R.J.

Harvey Inst. Corp.) for 2 minutes. Any labelled carbon in the plant part was converted to ^{14}C carbon dioxide and trapped in a vial containing liquid scintillation cocktail (R.J. Harvey ^{14}C cocktail). Vials were dark adapted for 30 minutes and counted in a liquid scintillation spectrometer (Mark III, Tracor Analytic). Recovery efficiency of the oxidizer was 97%. Counting efficiency of the entire system was 80%.

2.2.2 Experiment 1

To determine the pattern of ^{14}C assimilate distribution in a clone, a three-shoot plant system was used (Fig. 1). In separate trials, a shoot at each of the three possible positions was labelled. The plant was separated into its component parts and each part was assayed for radioactivity.

2.2.3 Experiment 2

To determine if the patterns observed in experiment 1 could be altered by disturbance, a shading experiment was conducted using a two-shoot plant system. A mature shoot at one of the positions was completely shaded with a 30 cm^2 piece of cardboard and two layers of black cloth. The other shoot was labelled 24 hours after the shade treatment was initiated. As a control, the same experiment was performed without the shade treatment. The plant was separated into its component parts and each part was assayed

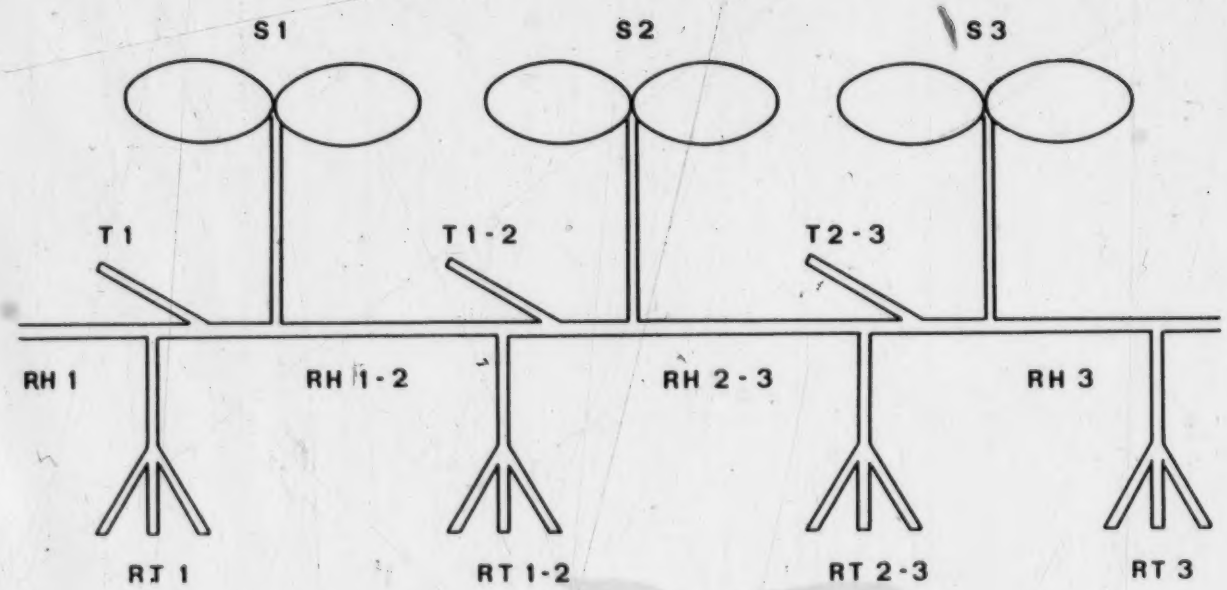

Fig. 1. Diagrammatic representation of a three-shoot plant system in Aralia nudicaulis L. The mature shoots (S) are numbered according to age from the youngest (1) to the oldest (3) based on the development of a clone. The rhizome (RH) sections are numbered according to the shoots to which they are connected. The roots (RT) are numbered according to the rhizome section from which they emerge. New developing rhizome tips (T) are numbered according to the rhizome section from which they emerge.

for radioactivity. Plant components are numbered according to the pattern outlined in the caption to Fig. 1.

2.3 Results

Most carbon assimilated by an individual shoot remained within that shoot for at least 24 hours (Fig. 2). Most of the exported carbohydrate moved into the rhizome adjacent to the labelled shoot. Smaller amounts of carbohydrate were taken up by roots and new rhizomes near the labelled shoot. There was little transport of carbohydrate to other parts of the clone.

Relative to their weight, roots and new developing rhizomes adjacent to the labelled shoot were the most successful in attracting assimilates (Table 1). The rhizome did not have as high a specific activity, but it had a larger biomass, therefore it accumulated a greater total amount of labelled carbon. Plant components basipetal to a shoot had higher specific activity than components located acropetal to a shoot (Table 1). Some carbohydrate was taken up by roots and new rhizomes farther away from the labelled shoot.

The pattern of carbohydrate translocation in a two-shoot system was altered by shading one shoot (Figs. 3 and 4). When shoot 1 was labelled, translocation of carbohydrate along the rhizome towards shoot 2 was increased by shading shoot 2 (Fig. 3).

Fig. 2. The pattern of ^{14}C assimilate distribution in a three shoot plant system. ^{14}C was supplied to: (a) shoot 1, (b) shoot 2, (c) shoot 3. Plant components are defined in the caption to Fig. 1. The shaded bars represent ^{14}C assimilates and the unshaded bars represent dry weight. The values are the means of two experiments.

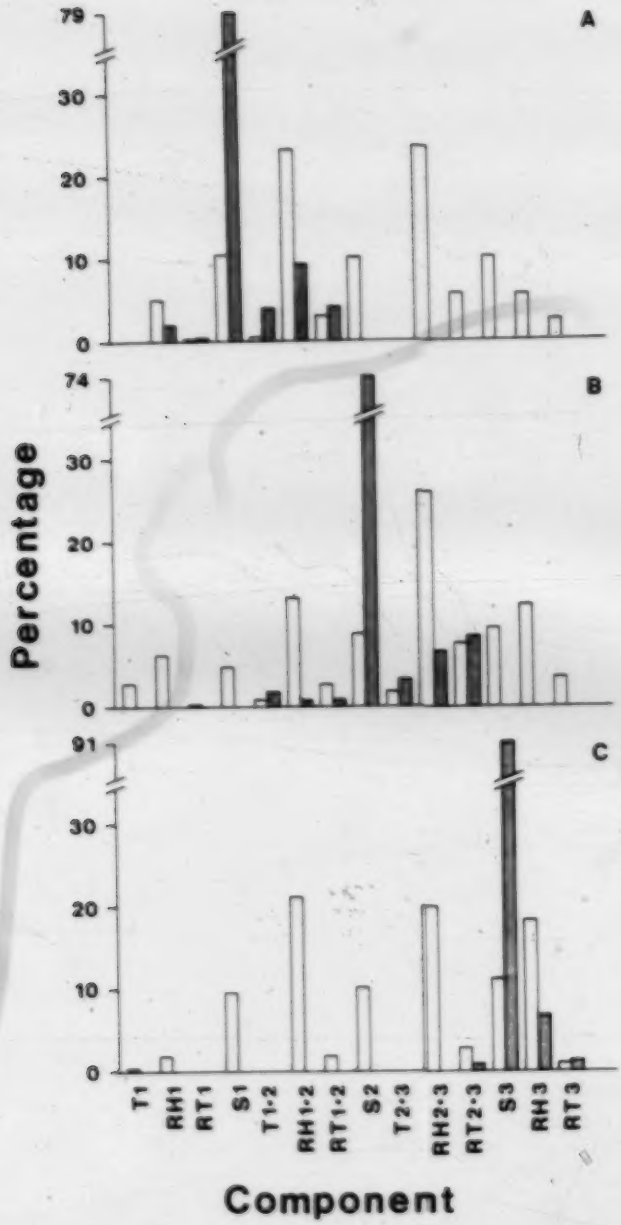
79
30
20
10
0
A
74
30
20
10
0
B
91
30
20
10
0
C
Percentage
T1
RH1
RT1
S1
T1-2
RH1-2
RT1-2
S2
T2-3
RH2-3
RT2-3
S3
RH3
RT3
Component

Table 1. Specific activity (DPM/mg) of the component plant parts in a three-shoot system. Plant components are defined in Fig. 1. Values are the means of two experiments.

Plant component	Label applied to shoot number		
	S1	S2	S3
T1	1	4	3
RH1	383	1	0
RT1	1638	0	86
S1	6120	5	2
T1-2	24776	1385	219
RH1-2	521	24	3
RT1-2	2128	294	73
S2	7	2252	1
T2-3	116	1021	29
RH2-3	3	109	8
RT2-3	91	591	480
S3	2	2	15217
RH3	0	1	500
RT3	1	111	1840

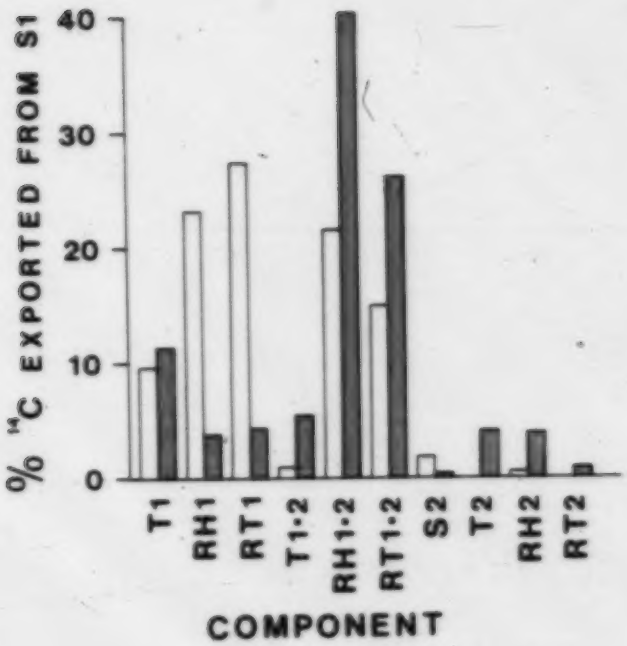

Fig. 3. The distribution pattern of ^{14}C assimilates exported by shoot 1 of a two-shoot plant system under control conditions and when shade has been applied to shoot 2. Unshaded bars represent the control and shaded bars represent the shade treatment. Plant components are defined in the caption to Fig. 1. Values are the means of two experiments.

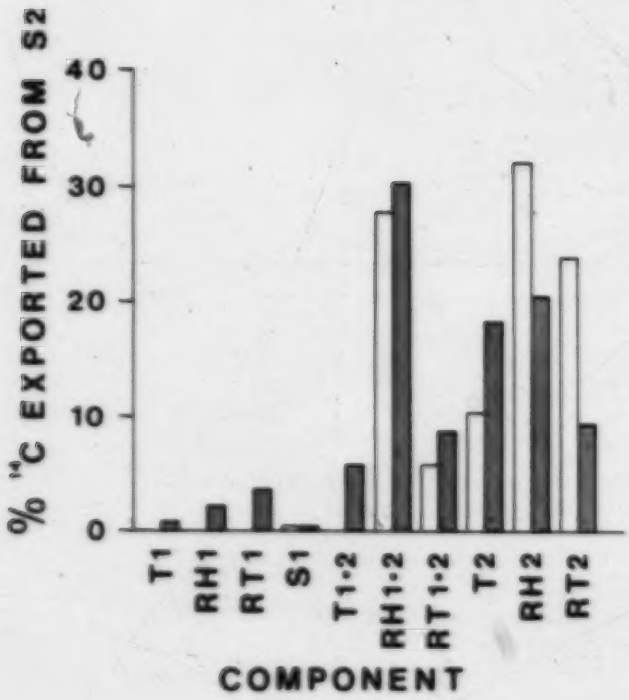

Fig. 4. The distribution pattern of ^{14}C assimilates exported by shoot 2 of a two-shoot plant system under control conditions and when shade has been applied to shoot 1. Unshaded bars represent the control and shaded bars represent the shade treatment. Plant components are defined in the caption to Fig. 1. Values are the means of two experiments.

Table 2. Changes in specific activity (DPM/mg) when shade is applied to a mature shoot in a two-shoot plant system. S1 was labelled 24 hours after shade was applied to S2. Plant components are defined in the caption to Fig. 1. Values are the means of two experiments. Within each row, values followed by the same letter are not significantly different ($P > .05$). * n = 1

Plant component	Control	Shade
T2	5 *	2485 *
RH2	2[a]	95[a]
RT2	3[a]	163[a]
S2	2[a]	11[a]
T1-2	1751 *	3195 *
RH1-2	152[a]	917[a]
RT1-2	285[a]	1828[b]
% Export from S1	11[a]	31[a]

Table 3. Changes in specific activity (DPM/mg) when shade is applied to a mature shoot in a two-shoot plant system. S2 was labelled 24 hours after shade was applied to S1. Plant components are defined in the caption to Fig. 1. Values are the means of two experiments. Within each row, values followed by the same letter are not significantly different ($P > .05$). * n = 1, ** no data

Plant component	Control	Shade
T1	**	1886 *
RH1	.3	653 *
RT1	**	657
S1	4[a]	80[a]
T1-2	23 *	4945
RH1-2	183[a]	859[b]
RT1-2	1206[a]	940[a]
% Export from S2	20[a]	39[a]

Plant components normally supplied with carbohydrate from the shaded shoot were supplied with carbohydrate from the labelled shoot upon disturbance. In general, the specific activity of plant components adjacent to shoot 2 was increased by shading shoot 2 (Table 2). However, the data were variable and the only significant difference between the treatments occurred for roots on the rhizome between shoots 1 and 2. Similar changes in the pattern of translocation were observed when shoot 2 was labelled and shoot 1 was shaded (Fig. 4, Table 3).

2.4 Discussion

The pattern of assimilate distribution in a three-shoot plant system indicates that mature, undisturbed shoots are physiologically independent. Carbohydrate produced by a shoot is used to support the growth of new rhizomes and roots adjacent to that shoot. In addition, a large amount of the assimilated carbohydrate is stored in the old rhizome sections near the shoot.

The pattern of assimilate distribution in *A. nudicaulis* can be interpreted in relation to the growth pattern of a clone. New rhizome segments, after a period of growth, eventually turn erect and develop into a new shoot (Bawa et al. 1982). This releases an axillary bud on the rhizome, a few centimeters behind the rhizome apex, from apical dominance. This bud grows out to replace the rhizome and continue the modular growth sequence of the plant (Bawa et

al. 1982). Carbohydrate produced by a shoot is predominantly translocated basipetally into the rhizome and associated plant components behind a shoot (Fig. 1). New developing rhizomes on this rhizome section have particularly high specific activity (Table 1). The new mature shoot produces the majority of the carbohydrate used to support the new rhizome growth (Fig. 1, Table 1). However, adjacent basipetal shoots do translocate some carbohydrate forward to apical rhizome sections and new developing rhizomes can attract carbohydrate from shoots some distance away (Fig. 1, Table 1).

The pattern of assimilate distribution in a two-shoot plant system follows the same general pattern observed for a three-shoot system (Fig. 3,4). Applying shade to one of the shoots in a two-shoot system alters the normal distribution pattern (Fig. 3,4). There was an increased amount of carbohydrate translocated to plant components adjacent to the shaded shoot (Fig. 3,4). Plant components normally supplied with carbohydrate from the shaded shoot (e.g., rhizome 1,2; roots 1,2) were supplied with carbohydrate from the labelled shoot upon disturbance.

The pattern of carbohydrate translocation in *A. nudicaulis* is similar to the pattern observed for a rhizomatous grass, *Poa pratensis*. In *P. pratensis*, carbohydrate produced by a shoot is used to support the growth of roots, tillers and new rhizomes adjacent to that shoot (Nyahoza et al. 1973, 1974). There is no translocation

to other parts of a clone. However, in response to defoliation, carbohydrate produced by an intact shoot is translocated to other parts of the plant.

The predominant basipetal translocation of assimilates in *A. nudicaulis* is different from the pattern observed in *Carex arenaria* despite similarity in the morphology of the two rhizome systems. In *C. arenaria* assimilates are translocated acropetally to developing shoots, roots and the rhizome apex (Tietema 1980, Noble and Marshall 1983). There was no translocation to older parts of the plant. However, this translocation pattern is associated with a different growth pattern than that observed for *A. nudicaulis*. The growth pattern of *C. arenaria* is described as phasic (Noble et al. 1979). The rhizome system is a continuum of biennial shoots in different phases of development from a juvenile phase at the leading edge of a clone to the senile and slack phases at the back of a clone where it is degenerating. While the morphology of *A. nudicaulis* is similar to *C. arenaria*, shoots in *A. nudicaulis* are much longer lived (often greater than 30 years). Translocation of carbohydrate to old sections of the rhizome may be necessary to store carbohydrate for growth in the subsequent growing season.

A shaded shoot in *A. nudicaulis* did not import a large amount of carbohydrate despite the changes observed in translocation pattern. Conversion of mature leaves into sinks has been observed under certain conditions. It is usually necessary to deplete the starch content of a mature

leaf and to limit the number of other competing sinks before a mature leaf will import assimilates from another leaf (Thrower 1974, Blechschmidt-Schneider 1984). The shaded shoot in this experiment was darkened 24 hours before an adjacent shoot was labelled, therefore it is doubtful that the starch content of the leaf was depleted. In addition, there were several other strong sinks present (eg. roots, new rhizomes) competing for assimilates. Therefore it is not surprising that very little assimilate was imported by the shaded shoot.

Despite the low import of assimilates into a mature shoot, the changes in translocation pattern observed after disturbance indicate the potential for individual shoots to be physiologically integrated. The changes in assimilate distribution could result in individual shoots being supported during chronic stress. In *Solidago canadensis*, shaded shoots that had intact rhizome connections to unshaded shoots showed no mortality for 7 weeks. Shaded shoots that had their connections severed, showed high mortality within a few days of the application of shade (Hartnett and Bazzaz 1983).

Further experiments need to be conducted with *Aralia nudicaulis* before the full significance of intraclonal connections between shoots can be realized. However, based on the present results, physiological processes occurring in the individual shoot should be considered in relation to the ecology of the entire clone.

3. Effect of gibberellic acid and light quality on flowering

3.1 Introduction

Aralia nudicaulis L. is a dioecious, herbaceous, perennial plant commonly found in the understory vegetation throughout the boreal forest of North America. Censuses in natural populations of *A. nudicaulis* have shown that in open areas (roadsides) the sex ratio of flowering shoots is approximately 1:1. In forested areas, however, a male-biased sex ratio is observed (Barrett and Helenurm 1981). In the more densely shaded areas within a forested site, fewer female shoots have been observed flowering relative to male shoots (Barrett and Thomson 1982). Barrett and Helenurm (1981) suggested that the flowering capacity of females may be reduced under low light regimes. This difference between the sexes may be due to the greater resource costs of reproduction in females because of fruit and seed production (Barrett and Helenurm 1981). In the forested sites, the reduced light intensity may not allow for enough carbohydrate production to offset this extra reproductive cost.

The passage of sunlight through a plant canopy not only reduces light intensity but also changes the spectral quality of light (Holmes and Smith 1977). The selective attenuation of sunlight by plant canopies results in a marked reduction in the blue and red regions of the daylight spectrum (Holmes and Smith 1977). The strong depletion of

the red wavelengths and relatively weak depletion of the far red wavelengths by a plant canopy may have significant effects on understory plants by altering their phytochrome photoequilibrium (Morgan 1981). Therefore, an alternative to the Barrett and Helenurm (1981) hypothesis is that the reduced flowering capacity of females in forests is due to the changes in the spectral quality of light under a forest canopy.

Some of the effects of phytochrome-controlled responses in plants may be mediated through the phytochrome-controlled release of gibberellins (Cooke et al. 1975, Morgan et al. 1980). Gibberellins have been shown to promote flowering in several plant species (Williams and Morgan 1979). Leshem and Ophir (1977) have shown that in two dioecious tree species, the females have higher endogenous gibberellin levels than male plants. Therefore, it is conceivable that lower female flowering in forests is due to the reduced red light under a canopy and therefore reduced gibberellin production. The high capacity for female flowering in roadsides is due to the high red light and high gibberellin production. The release of gibberellin may promote flowering directly, or it may lead to changes responsible for subsequent promotion. The male plants would be less sensitive to shade light because of their lower gibberellin requirements for promotion of flowering.

This chapter reports the results of a study conducted to test the hypothesis that flowering in *A. nudicaulis* is

affected by light quality changes mediated through phytochrome-controlled release of gibberellins. Applications of gibberellic acid and CCC, an inhibitor of GA biosynthesis, were made to plants to test their effect on flowering. In addition, two shade treatments were applied to plants to determine the effects of reduced intensity and altered spectral quality of light on flowering.

3.2 Materials and Methods

Aralia nudicaulis is a rhizomatous, perennial herb with a short, thick caudex bearing a single compound leaf. When reproductive, a shoot or ramet is subtended by a short scape which bears an umbellate inflorescence. Floral bud development is initiated the season before flowering occurs. Flowering is concomitant with leaf development in late May and early June in natural populations of the plant. Both the leaf and inflorescence develop from preformed buds on the caudex.

Experiments were conducted in a natural population of *A. nudicaulis* adjacent to reference stand 3 of the University of Alberta Hondo Research Laboratory near Hondo, Alberta. A description of the vegetation of the site may be found in Strong and La Roi (1983). A representative curve of the spectral photon distribution of sunlight penetrating the forest canopy in the study site is shown in Fig. 5. This curve was close to the mean of 8 measurements taken at random points at ground level within the forest.

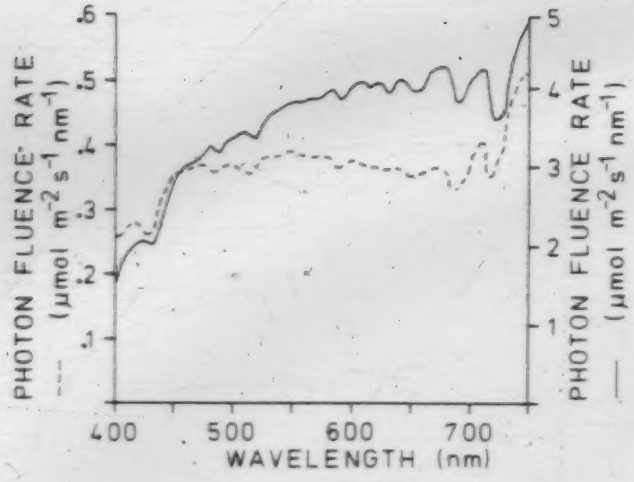

Fig. 5. The spectral photon distribution of full sunlight (solid line) and light penetrating the forest canopy in the study site (broken line). Note the different scales for each curve.

Measurements were made with a Li-Cor 1800 portable spectroradiometer between 1300-1400 hrs MDT on August 24, 1983. Mean photosynthetic photon flux density was 500 umol m^{-2} s^{-1} under the canopy and 990 umol m^{-2} s^{-1} outside the forest in a roadside clearing. The mean R:FR ratio was 0.84 under the canopy and 1.06 in the clearing.

In June 1983, 235 flowering female shoots and 145 flowering male shoots were marked with stakes. For 60 of the marked reproductive shoots of each sex and 60 non-flowering shoots the following information was recorded when each shoot was mature: length of the petiole; length (L) and width (W) of the 2 largest leaflets; and the number of leaflets/shoot (n). This information was used to derive a "performance index":

$$PI = n\ ((L_1W_1 + L_2W_2)/2)$$

This provided a fast non-destructive method to estimate shoot size. The PI is linearly related to leaf area (LA) and approximately twice as large ($PI = 1.80\ LA + 13.05$, $r = .99$, $P < .001$, Fig. 6).

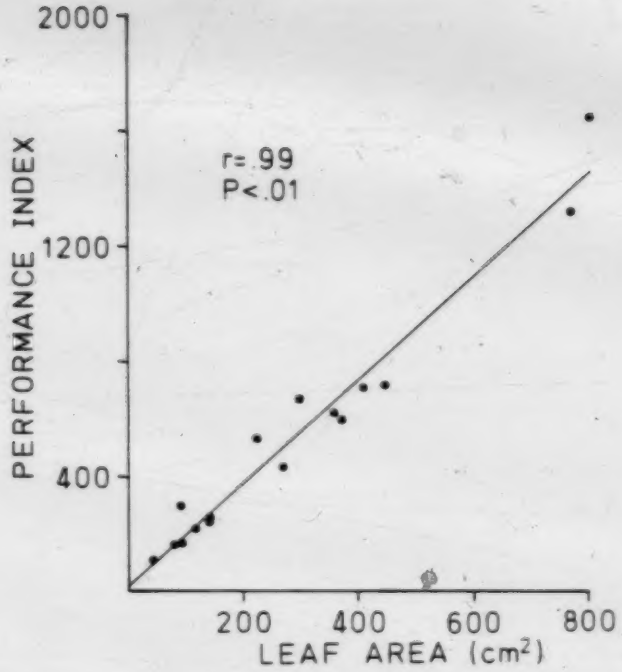

Fig. 6. The relationship between performance index and leaf area.

3.2.1 GA_3 and CCC application

The 60 male and 60 female shoots that were measured were used for growth substance treatments. Five treatments were performed using GA_3 (gibberellic acid; Sigma, St. Louis, Mo.; min. 90% pure) and CCC ((2-chloroethyl)trimethyammonium chloride; Aldrich, Milwaukee, Wis.; 98% pure). GA_3 was dissolved in 5 ml of 95% ethanol and made up to final concentration with water. The treatments were: (1) GA_3 10^{-3} M, (2) GA_3 10^{-4} M, (3) CCC 10^{-3} M, (4) CCC 10^{-3} M + GA_3 10^{-3} M, (5) CCC 10^{-3} M + GA_3 10^{-4} M, (6) water. Ten shoots of each sex were used for each treatment.

Growth substances were applied to the leaf as a spray until runoff occurred. In treatments 4 and 5, CCC was applied first and the leaf was allowed to dry before the GA_3 was applied. Applications were made on 4 dates during the growing season. The first application was after shoots were completely mature. Subsequent applications were made at 2, 3, and 4 week intervals. Growth substances were reapplied if rain occurred within 48 hours of an initial application.

3.2.2 Shading experiments

Eleven male and 11 female flowering shoots were used in the shading experiment. Shade was applied to shoots in the field using plexiglass domes that were equipped with filters. Domes were supported above the shoot by 4 wooden legs. The entire upper leaf surface of a shoot was covered

but air movement was possible below the dome which was suspended approximately 50 cm above the ground. Two types of shade treatments were used: (1) neutral density filter, and (2) minus red filter. The neutral density filter consisted of 2 layers of cheesecloth attached to the internal dome surface. This filter resulted in a uniform reduction in sunlight transmittance (Fig. 7c) with a total transmittance of 59.5% of full sun. The minus red filter consisted of a single sheet of Roscolux colored filter (#63, pale blue; Rosco, Port Chester, N.Y.) attached to the dome surface. This filter selectively absorbed red wavelengths and reduced the R:FR ratio to 0.74 (Fig. 7b). Total transmittance through the minus red filter was 63.4% of full sun. The spectral photon distribution of light transmitted through the experimental filters was measured with a Tectum Instruments QSM2500 quanta spectrometer under clear sky conditions on May 31, 1983 between 1200-1300 hrs MDT.

Seven male and female flowering shoots received the minus red treatment. Four male and female shoots received the neutral density treatment. Shoots were measured for the same size characteristics described above. Treatments were initiated when the shoots were mature and were continued until the leaf senesced at the end of the growing season.

All experimental treatments were performed during the summer of 1983 on the marked plants. In June 1984, shoots were measured as described above and the effect of the treatments on flowering was recorded.

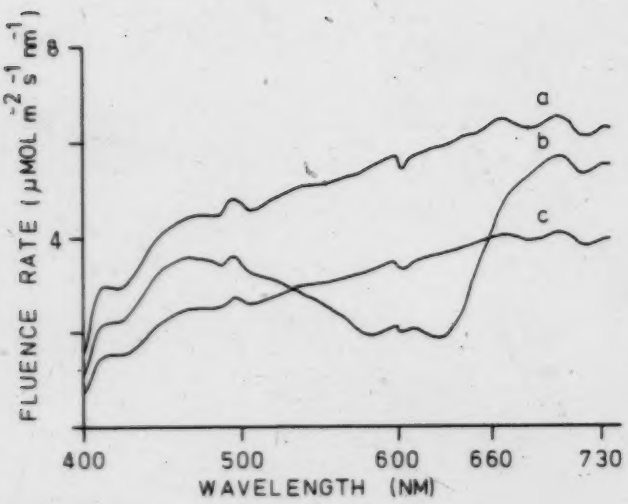

Fig. 7. The spectral photon distribution of: (a) full sunlight, and (b,c) light transmitted through the experimental light filters. Curve 'b' represents light transmitted through the minus red filter. Curve 'c' represents light transmitted through the neutral density filter.

Shoots were classified into three groups: (1) shoots with a leaf and inflorescence, (2) shoots with only a leaf, and (3) no shoot produced. Shoots that received a treatment were compared to the 164 female shoots and 74 male shoots that were marked but received no treatment. A Kolmogorov-Smirnov goodness of fit test was used to test for significant differences between the observed results of a treatment and an expected value based on the flowering pattern of the untreated shoots. The expected value was calculated as the proportion of untreated shoots grouped into each of the above 3 classes multiplied by the sample size for a treatment. If the test shows no significant difference between the observed results and the expected value, the treatment had no effect on the flowering pattern.

3.3 Results

3.3.1 Size of flowering and non-flowering shoots

Female and male flowering shoots were not significantly different in size for any of the characteristics measured (Table 4). Female flowering shoots were significantly larger than non-flowering shoots for all of the size characteristics measured. Male flowering shoots had longer petioles than non-flowering shoots but there was no significant difference between males and non-flowering shoots for leaflet number or performance index (Table 4).

Table 4. Mean values for the leaf characteristics of flowering and non-flowering Aralia nudicaulis L. shoots. Differences among shoot types were determined by nonparametric multiple comparison tests after Kruskal-Wallis analysis of variance. Within each row, values followed by the same letters are not significantly different ($P > .05$).

Characteristic	Female	Male	Non-Flowering
Petiole Length (cm)	24.3^{a}	26.9^{a}	21.9^{b}
Leaflet Number	14.3^{a}	13.1^{ab}	12.5^{b}
Performance Index	1040.8^{a}	1012.4^{ab}	852.7^{b}
N	60	60	60

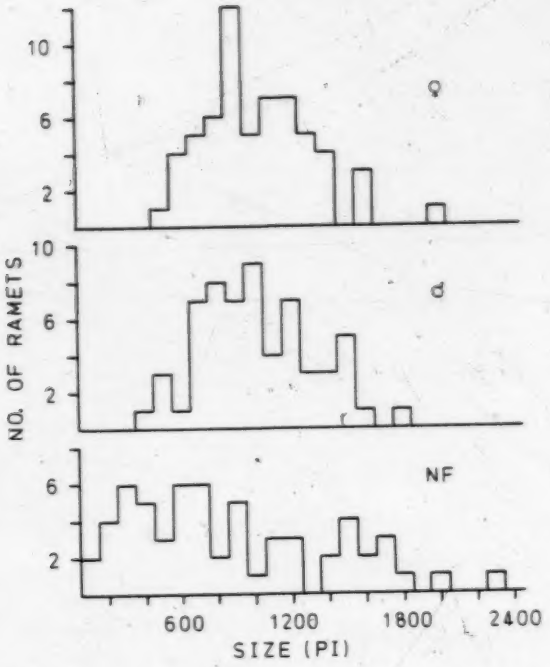

Fig. 8. Frequency distribution of size (performance index) in female, male, and non-flowering (NF) ramets of Aralia nudicaulis L. N = 60 for each group.

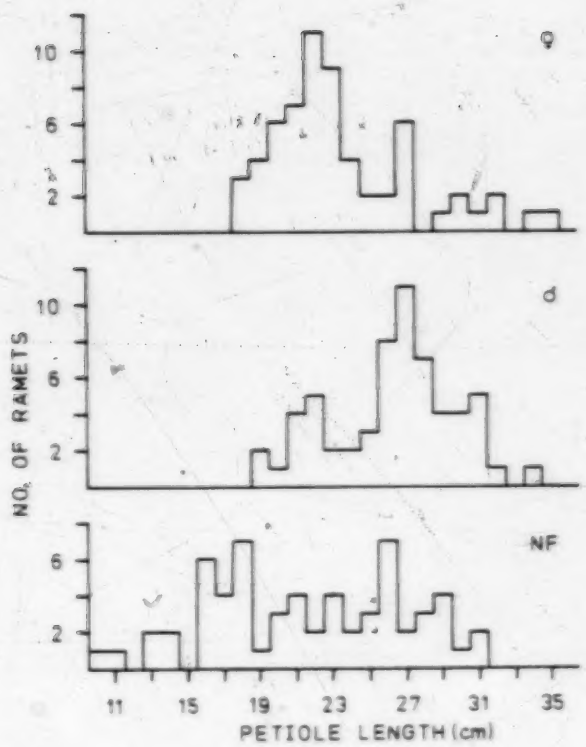

Fig. 9. Frequency distribution of petiole length in female, male and non-flowering (NF) ramets of Aralia nudicaulis L. N = 60 for each group.

Non-flowering shoots had a very broad size distribution relative to flowering shoots (Figs. 8, 9). There was a large number of non-flowering shoots in very small size classes but there was also a large number of non-flowering shoots in large size classes. The shoot with the largest PI measured in this sample was a non-flowering shoot (Fig. 9). Therefore the capacity to flower was not directly related to the size of a shoot.

3.3.2 Consecutive flowering pattern of untreated flowering shoots

Of the marked flowering shoots that were not treated in 1983, only 4.8% of the females flowered again in 1984, while 35.1% of the males flowered again in 1984 (Table 5). The majority of the male and female shoots only produced a leaf and several shoots did not appear again in 1984 (Table 5). The demographic behavior of individual shoots differed significantly between the sexes (Chi square=38.3, $P<.001$, 2 df; Table 5).

3.3.3 Effect of GA_3 and CCC on flowering

The normal developmental pattern was significantly altered in shoots that received the GA_3 10^{-3} M application. In both female and male shoots, the replacement bud at the base of a leaf grew out as a rhizome late in the 1983 growing season in response to the GA_3 treatment.

Table 5. Demographic behavior of Aralia nudicaulis L. flowering ramets. Flowering ramets were marked in 1983 and classified into the three classes shown below in 1984. The response of the sexes is significantly different (Chi square = 38.3, 2 df, $P < .001$).

	Leaf and Inflorescence	Leaf	No Leaf	Total
Male	26 (35.1%)	42 (56.8%)	6 (8.1%)	74
Female	8 (4.8%)	140 (85.4%)	16 (9.8%)	164

These shoots did not produce a leaf in 1984 and were excluded from further analysis.

The remaining growth substance treatments did not significantly change the response of treated shoots from the pattern observed in untreated shoots (Table 6). Female shoots did not flower in any of the treatment groups. Approximately 80% of the female shoots produced a leaf in 1984, while approximately 20% of the shoots did not appear in 1984 (Table 6). Flowering occured in 30% of male shoots while the remaining 70% of male shoots only produced a leaf (Table 6). In the female and male shoots that received water application, the pattern was slightly different from the shoots that received the growth substance application (Table 6).

3.3.4 Effect of shading on flowering

The two shade treatments had no significant effect on flowering in treated shoots relative to untreated shoots (Table 7). Female shoots did not flower in either the minus red or neutral density treatment. All shaded female shoots produced a leaf in 1984 (Table 7). Two male shoots in the minus red treatment flowered, while the remaining 5 shoots produced a leaf. All four of the male shoots in the neutral density treatment produced a leaf in 1984.

Table 6. Effect of GA_3 and CCC application on flowering in female and male shoots of Aralia nudicaulis L. None of the treatments are significantly different from expected values based on the response of untreated flowering shoots ($P > .05$, Kolmogorov-Smirnov test for goodness of fit). See methods for further explanation.

Female Shoots		Treatment			
Class	Expected	Water	CCC (10^{-2}M)	GA_3 (10^{-4}M)	CCC+GA_3 (10^{-2}M+10^{-4}M)
Leaf and Inflorescence	.48	0	0	0	0
Leaf	8.54	10	9	8	8
No Leaf	.98	0	1	2	2

Male Shoots		Treatment			
Class	Expected	Water	CCC (10^{-2}M)	GA_3 (10^{-4}M)	CCC+GA_3 (10^{-2}M+10^{-4}M)
Leaf and Inflorescence	3.51	6	3	3	3
Leaf	5.68	4	7	7	7
No Leaf	.81	0	0	0	0

Table 7. Effect of shade treatments on flowering in female and male shoots of Aralia nudicaulis L. None of the treatments are significantly different from expected values based on the response of untreated flowering shoots ($P > .05$, Kolmogorov-Smirnov test for goodness of fit). See methods for further explanation.

Female Shoots

Class	Expected	Minus Red Filter	Expected	Neutral Density Filter
Leaf and Inflorescence	.3	0	.2	0
Leaf	6.0	7	3.4	4
No Leaf	.7	0	.4	0

Male Shoots

Class	Expected	Minus Red Filter	Expected	Neutral Density Filter
Leaf and Inflorescence	2.4	2	1.4	0
Leaf	4.0	5	2.3	4
No Leaf	.6	0	.3	0

3.3.5 Effect of GA_3, CCC and shading on shoot size

There was no significant difference among growth substance treatments or between sexes in the percentage change in shoot performance index from 1983 to 1984 (Tables 8, 9). Two way analysis of variance indicated that there was no difference between sexes but that there was a difference among treatments in the percentage change in petiole length between 1983 and 1984 (Tables 10, 11). However, Student-Newman-Kuels multiple comparison test indicated no significant difference among treatments for mean petiole length (Table 11).

Combining all growth substance treatments, female shoots had approximately a 10% reduction in both petiole length and performance index from 1983 to 1984. Male shoots had approximately a 15% reduction in petiole length but only a 3% reduction in performance index from 1983 to 1984 (Tables 9, 11).

In female shoots, the neutral density filters caused a significantly greater reduction than minus red filters in % change in petiole length and performance index (Tables 12, 13). There was no significant difference in effect between shade treatments on male shoots for either size measurement (Tables 12, 13). In addition, there was no significant difference between female and male shoots in their response to either neutral density or minus red filters for either size measurement (Tables 12, 13).

Table 8. Two-way ANOVA of the effect of sex and growth substance treatment on the % change in performance index in Aralia nudicaulis L. between 1983 and 1984.

SOURCE	DF	SS	MS	F
Sex	1	333	333	.22 NS
Treatment	3	7394	2465	1.65 NS
Interaction	3	2433	811	.54 NS
Error	56	83463	1490	
Total	63	93623		

Table 9. Effect of growth substance application on the % change in performance index in Aralia nudicaulis L. between 1983 and 1984. There is no significant difference among treatments based on analysis of variance.

	Treatment				
	Water	CCC (10^{-2}M)	CCC+GA_3 (10^{-2}M+10^{-4}M)	GA_3 (10^{-4}M)	All
Male $\bar{x}$	-4.51	-7.72	-3.43	2.2	-3.36
n	10	10	10	10	40
Female $\bar{x}$	12.43	-2.09	-30.59	-24.36	-9.55
n	10	9	8	8	35

Table 10. Two-way ANOVA of the effect of sex and growth substance treatment on the % change in petiole length in Aralia nudicaulis L. between 1983 and 1984.

SOURCE	DF	SS	MS	F
Sex	1	690	690	3.27 NS
Treatment	3	2607	869	4.12 *
Interaction	3	27	9	.04 NS
Error	56	11828	211	
Total	63	15152		

Table 11. Effect of growth substance application on the % change in petiole length in Aralia nudicaulis L. between 1983 and 1984. There is no significant difference among treatments based on Student-Newman-Kuels tests after analysis of variance.

	Treatment				
	Water	CCC (10^{-2}M)	CCC+GA_3 (10^{-2}M+10^{-4}M)	GA_3 (10^{-4}M)	All
Male $\bar{X}$	-24.89	-21.80	-7.53	-8.95	-15.79
n	10	10	10	10	40
Female $\bar{X}$	-16.58	-16.55	-2,04	-2.15	-9.95
n	10	9	8	8	35

Table 12. Effect of shading on % change in petiole length in Aralia nudicaulis L. between 1983 and 1984. Within a row, values followed by a different letter are significantly different (t-test, $P < .05$). There is no significant difference between sexes for either treatment (t-test, $P > .05$).

	Treatment		
	Neutral Density Filter	Minus Red Filter	All
Male $\bar{x}$	-31.3^a	-15.14^a	-21.02
n	4	7	11
Female $\bar{x}$	-15.15^a	$.83^b$	-5.56
n	4	6	10

Table 13. Effect of shading on % change in performance index in Aralia nudicaulis L. between 1983 and 1984. Within a row, values followed by a different letter are significantly different (t-test, $P < .05$). There is no significant difference between sexes for either treatment (t-test, $P > .05$).

	Treatment		
	Neutral Density Filter	Minus Red Filter	All
Male $\bar{X}$	-13.26[a]	12.49[a]	3.12
n	4	7	11
Female $\bar{X}$	-55.35[a]	1.45[b]	-21.27
n	4	6	10

When the results of the two shade treatments were combined and compared to the combined results for the growth substance treatments, there was no significant difference between shading and growth substance treatments in female or male shoots for either size measurement.

3.4 Discussion

Flowering in *A. nudicaulis* was not affected by the GA, or CCC applications, or the two shade treatments. None of the experimental treatments altered the flowering pattern of treated shoots from that observed in the untreated flowering shoots. Therefore, flowering is not directly affected by phytochrome-controlled release of gibberellins in *A. nudicaulis*.

Since the shade treatments had no effect on flowering, the Barrett and Helenurm (1981) hypothesis that reduced light intensity affects flowering is not supported either. An alternative explanation for the control of flowering in *A. nudicaulis* is required.

Flowering in consecutive seasons is affected by what may be called the cost of reproduction. Just a small percentage of shoots flower in consecutive seasons with female shoots more affected than male shoots by this reproductive cost. Only 4.8% of females compared to 35.1% of males flowered in consecutive seasons (Table 5). In addition, shoots are generally smaller in size the season after flowering (Tables 9, 11, 12, 13). The male biased sex

ratios may be a result of the differences in frequency of flowering between the sexes (Barrett and Helenurm 1981, Bawa et al. 1982).

It is generally assumed that female function in reproduction requires a heavier investment of resources than male function (Lovett Doust and Lovett Doust 1983). Barrett and Helenurm (1981) have shown that biomass allocated to reproduction in male flowering shoots of *A. nudicaulis* is significantly higher than in females at peak flowering. However, after flowering, male inflorescences die while female shoots continue to allocate biomass to fruit production for 6 more weeks. Biomass is a good indicator of the carbohydrate content of a plant structure but it is a poor predictor of nutrient content (Abrahamson and Caswell 1982). At present, there is little information on what resources actually limit plant reproduction in perennial plants.

One hypothesis presented to explain the control of flowering is the "nutrient diversion hypothesis", which states that the shoot apical meristem is deprived of nutrients during vegetative development and must receive a higher level of nutrients before a switch to reproductive development can occur (Sachs 1977, Sachs and Hackett 1983). Growth substances and environmental factors are believed to have indirect control over flowering by increasing nutrient availability to the apical meristem and by reducing the competitive abilities of other sinks in the plant.

At present, it is impossible to distinguish between the nutrient diversion hypothesis and floral hormone hypotheses which suggest that growth substances have morphogenetic influences on meristems (Sachs and Hackett 1983). However, there are studies which suggest that nutrient availability may be the critical factor controlling flowering in perennial plants. In *Limonium vulgare*, a salt marsh perennial, environmental conditions generally require a large allocation of carbon and nitrogen to plant maintainance (Jefferies et al. 1979). Flowering does not occur every year in these plants. If flowering does occur, the development of seeds may be aborted if growing conditions deteriorate during the season (Jefferies et al. 1979). If nitrogen fertilizer is applied to plants in the field, flowering and seed producton is increased while vegetative growth is not significantly different from control plots (Jefferies and Perkins 1977). This suggests that flowering is restricted to years when conditions are favorable. Alternatively, nutrients may be taken up gradually over a period of time and sequestered until nutrient content is high enough for flowering to occur.

The small number of shoots that flowered in consecutive years and the reduced shoot size after flowering suggests that flowering is a large drain on resources in *A. nudicaulis*. The amount of nutrients allocated to flowering can be high particularly after fruit production is initiated in females (Lovett Doust and Harper 1980). Therefore if

nutrient availability is normally low in natural populations, nutrient shortages could be the main factor limiting flowering in *A. nudicaulis*. Fertilization of plants in the field would help to test this hypothesis.

4. Intrapopulation variation in secondary sex characteristics

4.1 Introduction

The effects of pollinator behavior and sexual selection have recently been emphasized as major factors influencing the evolution of plant sexual systems (Willson 1979, Bawa 1980, Bawa and Beach 1981). Sexual selection is a form of natural selection where there is competition for mates in one sex and mate choice in the other sex (Willson 1979). As applied to plants, sexual selection is thought to operate when female reproductive success is limited by resources and male reproductive success is limited by the number of ovules fertilized (Willson 1979). If female reproductive success is pollen limited, sexual selection will not operate (Willson 1982). However, the selection potential of pollinator behavior on plant characteristics is most effective when pollination limits seed production (Schemske 1983).

Pollinator behavior and sexual selection have also been suggested as major factors influencing the development of many secondary sex characteristics (Lloyd and Webb 1977). Secondary sex characteristics are defined as any difference between males and females in characteristics other than sex (Lloyd and Webb 1977). While sexual dimorphism in plants may be the biproduct of physiological or genetic aspects of primary sex determination, Lloyd and Webb (1977) have suggested that many secondary sex characteristics are a

result of male and female plants adapting to their particular reproductive roles. At present there are few studies that have demonstrated the adaptive significance of secondary sex characteristics in plants (Valdeyron and Lloyd 1979, Bullock and Bawa 1981). One method to test the adaptive significance of a characteristic is to determine how variation in that characteristic affects fitness.

Aralia nudicaulis is a dioecious plant species that is sexually dimorphic for several characteristics (Barrett and Helenurm 1981, Bawa et al. 1982). One characteristic is the asynchronous flowering phenology of the sexes. Barrett and Helenurm (1981) have shown that *A. nudicaulis* females start to flower before males both at the level of ramets and flowers in a population. This flowering pattern is unusual because in virtually all other reported cases where there are differences in the flowering phenology between sexes of dioecious plants, males have been shown to flower earlier than females (Bawa 1983). Barrett and Helenurm (1981) suggested that early female flowering in *A. nudicaulis* is associated with competition between the sexes for pollinators. Females have smaller inflorescences than males in *A. nudicaulis* and therefore may be less attractive to bumble bees, the major pollinators (Barrett and Helenurm 1981, Barrett and Thomson 1982).

For pollinators to influence flowering time, pollination intensity must limit seed set and individual plants must exhibit a differential seed set as a function of

their flowering time (Gross and Werner 1983). Recent studies have shown flowering time to influence pollination and seed set (Augsperger 1981, Gross and Werner 1983, Schmitt 1983). However, several other factors such as inflorescence size (Willson and Price 1977), plant spatial pattern (Wyatt and Hellwig 1979, Barrett and Thomson 1982), and plant size (Solbrig 1981, Wolfe 1983) also affect pollinator visitation rate and fecundity.

The purpose of this study was to determine how intrapopulation variation in secondary sex characteristics affects pollination and seed set in *Aralia nudicaulis*. Specifically the effect of (1) flowering time, (2) inflorescence size, (3) plant spatial pattern, and (4) ramet size on pollination and seed set were studied. An attempt was made to identify the interactions and tradeoffs among factors affecting the evolution of secondary sex characteristics in *A. nudicaulis*.

4.2 Materials and Methods

Aralia nudicaulis is a rhizomatous, perennial herb with a short, thick caudex bearing a single compound leaf. When reproductive, a leaf is subtended by a short scape which bears an umbellate inflorescence. *Aralia nudicaulis* is dioecious. The male flowers have five long stamens with bright white anthers and short styles with a non-functional pistil. The female flowers have five long styles and short stamens with non-functional anthers. Floral development is

concomitant with leaf development in late May and early June in natural populations of the plant.

The study was conducted in a natural population of *A. nudicaulis* adjacent to reference stand three of the University of Alberta Hondo Research Laboratory near Hondo, Alberta. A description of the vegetation and site characteristics of the study area may be found in Strong and La Roi (1983). The study area was located where there was a great deal of intermingling of male and female flowering ramets. The floral sex ratio in the study area was approximately one to one.

In late May of 1983, 164 female ramets and 74 male ramets of *A. nudicaulis* were marked with stakes. At two day intervals each marked ramet was inspected to determine the number of ramets that were in flower (i.e. ramets that had at least one flower at anthesis) and the number of flowers at anthesis within individual inflorescences. A flower was considered to be at anthesis when the styles diverged in females and when the anthers dehisced in males (Barrett and Helenurm 1981). The total number of flowers per inflorescence was also recorded.

After all female ramets had completed flowering, their infructescences were covered to prevent loss of fruit with drawstring bags made from nylon bridal veil mesh. The fruit was collected in August when it was mature. Seeds were extracted from the fruit and classified as filled or unfilled by pressing on them with a metal probe. Filled

seeds were counted and weighed after drying at 45 C for 48 hours. Mean seed weight was calculated for each ramet by dividing the total weight of all a ramet's seeds by the number of seeds weighed.

To determine if lack of pollination was limiting seed production, randomly selected ramets flowering at different times during the season were hand-pollinated to supplement any natural pollination the plants received. Hand-pollination was performed when all flowers in an inflorescence were at anthesis. The pollen was applied by brushing a female inflorescence with two male inflorescences picked from areas adjacent to the study plot. The effectiveness of this technique was tested by hand-pollinating ten female inflorescences that had been bagged while still in the bud stage. In addition, five female inflorescences were bagged while in the bud stage and were not hand-pollinated. Of the bagged inflorescences, those that received hand pollination had a mean of 80.2% fruit set and a mean of 125.3 seeds per inflorescences while those that were not hand pollinated had a mean of 4.6% fruit set and did not produce any seeds. Therefore the pollination technique was effective and there is no apomictic seed production in *A. nudicaulis*.

In late May 1984, the marked ramets were censused to determine the number of ramets which flower in consecutive years. Additional new ramets were marked to replace ramets that did not have inflorescence buds. In June 1984, 120

female ramets and 97 male ramets were inspected every two days to determine the number of ramets in flower and the date when all flowers in an inflorescence were at anthesis. Hand pollination, fruit collection and seed counts were performed as described above.

In order to determine the relationship between ramet size and fecundity, the following information was recorded for the 120 female ramets marked in 1984 when each ramet was mature: length of the petiole; length (L) and width (W) of the two largest leaflets; and the number of leaflets per ramet (n). This information was used to derive a "performance index":

$$PI = n\ ((L_1W_1 + L_2W_2)/2)$$

This provided a fast non-destructive method to estimate shoot size. The PI is linearly related to leaf area (LA) and approximately twice as large ($PI = 1.8\ LA + 13.05$, $r = .99$, $P < .001$, Fig. 6, p. 32). The PI and petiole length were tested for association with the seed set of the individual ramets using linear regression.

In order to determine the relationship between the spatial pattern of the sexual morphs and fecundity, the distance from 51 naturally pollinated female ramets to the nearest flowering male ramet was measured. This distance measurement was tested for association with the seed set of the individual ramets using linear regression.

4.3 Results

4.3.1 Inflorescence size

Male inflorescences had on average twice as many flowers as female inflorescences (99.6 vs 49.8, $t = 25.2$, $P < .001$, Fig. 10). Despite the differences in flower number, the majority of male and female inflorescences had three umbels (Table 14). The difference in flower number between the sexes was predominantly due to the fewer flowers per umbel in females. However, the frequency distribution of umbel number also differed significantly between the sexes. Females had a higher frequency of two umbels and males had a higher frequency of four umbels per inflorescence (Table 14).

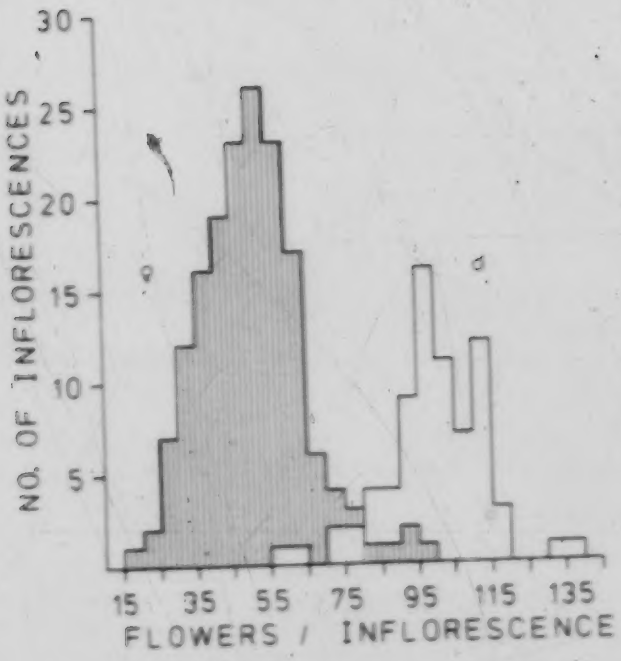

Fig. 10. Frequency distribution of flower number in female and male inflorescences of Aralia nudicaulis L.

Table 14. Frequency of umbel number in Aralia nudicaulis L. The distribution is significantly different between the sexes (Chi square = 27.6, df = 2, $P < .001$).

	Umbels per Inflorescence			
	2	3	4	Total
Female	45 (27.4%)	117 (74.3%)	2 (1.3%)	164
Male	1 (1.4%)	67 (90.5%)	6 (8.1%)	74

In female ramets, some of the population variation in the number of flowers per inflorescence is associated with flowering date. Female ramets that reach full bloom early in the season have on average fewer flowers per inflorescence than female ramets that bloom later in the season (Table 15, 16).

4.3.2 Flowering phenology

Female ramets began flowering on June 7 in 1983 and on June 4 in 1984 (Fig. 11, 12). In both years females started to flower before males. The cumulative flowering curves for female ramets are significantly displaced from that of the male ramets (Fig. 11, $D = .348$, $P < .001$; Fig. 12, $D = .608$, $P < .001$; Kolomogorov-Smirnov two sample test). A similar pattern is observed when flowering phenology is presented as the total number of flowers at anthesis on a given day (Fig. 13). The peak flowering time of females was two days earlier than males. In addition to the differences in phenology between the sexes, there was considerable variation in the date at which individual female ramets reached full bloom (Table 15, 16).

Table 15. Flower number, seed production and mean seed weight in Aralia nudicaulis L. in 1983. Within a row, values followed by the same letter are not significantly different ($P > .05$) based on Student-Newman-Kuels tests after analysis of variance. Values within a column are not significantly different ($P > .05$) based on a t-test.

Characteristic	Date of full bloom					
	June 11	June 13	June 15	June 17	June 19	All
Flower number						
$\bar{X}$	44.9[a]	45.7[a]	51.8[a]	57.6[b]	59.0[b]	
n	16	10	22	26	9	
Seed number						
$\bar{X}$ control	46.8[a]	140.8[b]	120.3[b]	139.1[b]	82.7[ab]	105.5
n	13	6	15	16	9	59
$\bar{X}$ sup. pollen	81.7[a]	119.7[a]	114.9[a]	111.0[a]	-	109.9
n	3	4	7	10	-	24
Seeds/flower						
$\bar{X}$ control	0.99[a]	2.72[b]	2.37[b]	2.21[b]	1.40[a]	1.91
n	13	6	15	16	9	59
$\bar{X}$ sup. pollen	1.50[a]	2.64[a]	2.15[a]	2.17[a]	-	2.15
n	3	4	7	10	-	24
Mean seed wt. (mg)						
$\bar{X}$ control	5.02[a]	5.56[b]	5.64[b]	4.80[a]	4.72[a]	5.13
n	13	6	15	16	9	59
$\bar{X}$ sup. pollen	5.04[a]	5.44[a]	5.00[a]	5.10[a]	-	5.12
n	3	4	7	10	-	24

Table 16. Flower number, seed number and mean seed weight in Aralia nudicaulis L. in 1984. Within a row, values followed by the same letter (a,b,c) are not significantly different ($P > .05$) based on Student-Newman-Kuels tests after analysis of variance. Within a column, values followed by the same letter (x,y) are not significantly different ($P > .05$) based on a t-test.

Characteristic	Date of full bloom					
	June 6	June 8	June 10	June 12	June 14	All
Flower number						
$\bar{x}$	45.8^{ab}	44.8^{ab}	44.1^{a}	54.2^{bc}	57.0^{c}	
n	18	13	33	26	30	
Seed number						
$\bar{x}$ control	61.6^{ax}	68.5^{ax}	66.1^{ax}	112.8^{ax}	126.7^{bx}	90.5^{x}
n	9	6	18	13	15	61
$\bar{x}$ sup. pollen	124.1^{ax}	81.7^{ax}	115.7^{ax}	162.1^{ax}	152.7^{ax}	132.6^{y}
n	9	7	15	13	15	59
Seeds/flower						
$\bar{x}$ control	1.52^{ax}	1.49^{ax}	1.41^{ax}	1.98^{ax}	2.13^{ax}	1.69^{x}
n	9	6	18	13	15	61
$\bar{x}$ sup. pollen	2.49^{ax}	1.60^{ax}	2.40^{ay}	2.90^{ay}	2.78^{ax}	2.52^{y}
n	9	7	15	13	15	59
Mean seed wt. (mg)						
$\bar{x}$ control	4.88^{ax}	4.86^{ax}	4.02^{ax}	4.06^{ax}	3.85^{ax}	4.19^{x}
n	9	6	18	13	15	61
$\bar{x}$ sup. pollen	4.94^{ax}	4.94^{ax}	4.67^{bx}	4.46^{bx}	4.05^{bx}	4.54^{x}
n	9	7	15	13	15	59

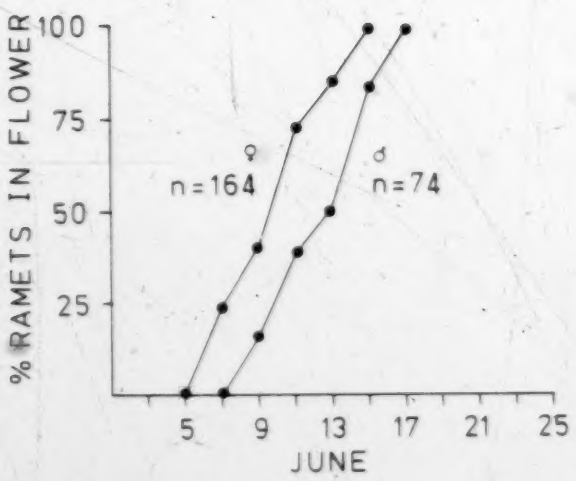

Fig. 11. Cumulative flowering curves for female and male ramets in a natural population of Aralia nudicaulis L. during 1983.

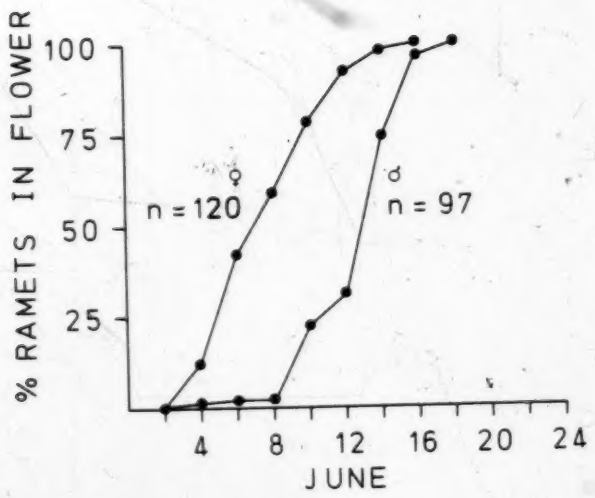

Fig. 12. Cumulative flowering curves for female and male ramets in a natural population of Aralia nudicaulis L. during 1984.

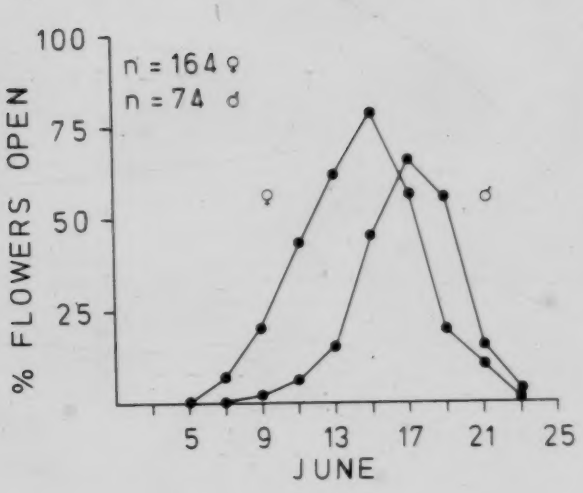

Fig. 13. Flowering curves for female and male flowers of Aralia nudicaulis L. in a natural population during 1983.

4.3.3 Relations of flowering phenology and pollination intensity with seed set

In 1983, naturally pollinated females that flowered at the peak male bloom (June 17) or from two to four days before the peak male bloom produced significantly more seeds than individuals that flowered very early (Table 15). Individuals that flowered very late produced an intermediate number of seeds not significantly different from any of the other groups (Table 15). A similar pattern is observed for seed set per flower in 1983. Individuals that flowered at the peak male bloom or from two to four days earlier produced more seeds per flower than individuals that flowered very early or very late (Table 15). In addition, individuals that flowered from two to four days before the peak male bloom had higher mean seed weight than individuals that flowered very early or very late (Table 15). Therefore there was no apparent tradeoff between the number of seeds produced and seed size.

In the group that received supplemental pollination, there was no significant increase in the total number of seeds produced or seed set per flower on any date throughout the 1983 season (Table 15). Therefore there was no evidence to suggest that pollination intensity limited seed set. However, several plants that received supplemental pollination, in particular all those of the June 19 group, were destroyed before their fruit could be collected (Table 15).

In 1984, naturally pollinated females that flowered very late in the season produced significantly more seeds than individuals that flowered at any other time during the season (Table 16). There was no significant difference in seed set per flower or mean seed weight among individuals that flowered at different times (Table 16). As was indicated by the 1983 data, there was no apparent tradeoff between the number of seeds produced and seed size.

In the group that received supplemental pollination, there was a general increase in the number of seeds produced relative to the naturally pollinated inflorescences (Table 16). While supplemental pollination did not result in a significant increase in total seed production on any one date, when all the flowering dates are combined there was a significant difference between individuals that received supplemental pollination and the naturally pollinated individuals (Table 16). In addition, individuals that received supplemental pollination on June 10 and 12 produced significantly more seeds per flower than did naturally pollinated inflorescences (Table 16). Therefore pollination intensity did limit seed set in 1984.

4.3.4 Correlation of ramet size with seed set

Female ramets that reached full bloom early in the season were larger than ramets that bloomed later in the season (Table 17). The size of female ramets was negatively correlated with seed set per flower (Table 18). However, the

number of flowers per inflorescence was also negatively correlated with petiole length (Table 19). The negative correlation between ramet size and seed set was likely a result of the negative correlation of ramet size and flower number. Ramets with a large number of flowers produced more seeds per flower in 1984 (see below).

4.3.5 Correlation of inflorescence size with seed set

There was a significant positive relationship between number of flowers per inflorescence and total seed production and seed set per flower in 1983 and 1984 (Tables 20, 21, 22, 23). In both years the significance of this relationship varied throughout the flowering season. The correlation between flower number and seed set per flower was significant only in the early part of the season in 1983 (Table 21) and only at the peak female bloom (June 10) in 1984 (Table 23).

4.3.6 Relationship between spatial pattern and seed set

There was no significant relationship between the distance to the nearest flowering male ramet and seed set per flower for naturally pollinated female ramets (Table 24). No significant relationship was apparent if the ramets were grouped according to the date of full bloom or if they were grouped according to flower number (Table 24).

Table 17. Mean size-characteristics of female Aralia nudicaulis ramets that reached full bloom on different dates in 1984. Within a row, values followed by the same letter are not significantly different ($P > .05$) based on Student-Newman-Kuels' tests after analysis of variance.

Characteristic	Date of full bloom				
	June 6	June 8	June 10	June 12	June 14
Performance Index	1685.3^{a}	1524.5^{ab}	1369.1^{b}	1245.0^{bc}	1068.2^{c}
Petiole Length (cm)	25.5^{a}	24.5^{ab}	23.7^{ab}	22.1^{bc}	21.6^{c}
n	18	13	33	26	30

Table 18. Summary of linear regressions relating shoot size (independent variable) to seed set per flower (dependent variable) in Aralia nudicaulis L.

Characteristic	N	Slope	Intercept	r^2	P
Performance Index	120	-0.001	2.9	0.042	.0254
Petiole Length	120	-0.195	6.6	0.272	.0001

Table 19. Summary of linear regressions relating shoot size (independent variable) to number of flowers per inflorescence (dependent variable) in Aralia nudicaulis L.

Characteristic	N	Slope	Intercept	r^2	P
Performance Index	120	-0.002	53.1	0.006	.3908
Petiole Length	120	-1.583	86.6	0.170	.0001

Table 20. Summary of linear regressions relating flower number (independent variable) to total seed production (dependent variable) in Aralia nudicaulis L. in 1983.

Flowering Date	N	Slope	Intercept	r^2	p
June 11	16	3.69	-122.2	0.528	.0014
June 13	10	4.49	-73.13	0.790	.0006
June 15	22	1.96	16.8	0.157	.0682
June 17	26	2.72	-28.2	0.583	.0001
June 19	9	1.99	-34.5	0.281	.1423
All Groups	83	2.76	-37.6	0.394	.0001

Table 21. Summary of linear regressions relating flower number (independent variable) to seed set per flower (dependent variable) in Aralia nudicaulis L. in 1983.

Flowering Date	N	Slope	Intercept	r^2	P
June 11	16	0.05	-1.23	0.321	.022
June 13	10	0.06	0.08	0.402	.0489
June 15	22	-0.003	2.44	0.001	.8894
June 17	26	0.007	1.81	0.024	.4480
June 19	9	-0.000	1.40	0.000	1.0000
All Groups	83	0.016	1.14	0.05	.0414

Table 22. Summary of linear regressions relating flower number (independent variable) to total seed production (dependent variable) in Aralia nudicaulis L. in 1984.

Flowering Date	N	Slope	Intercept	r^2	p
June 6	9	4.79	-141.1	0.54	.025
June 8	6	7.84	-290.7	0.57	.0821
June 10	18	4.18	-114.5	0.48	.002
June 12	13	3.79	-89.9	0.66	.0001
June 14	15	2.13	-0.4	0.19	.107
All Groups	61	3.70	-92.8	0.52	.0001

Table 23. Summary of linear regressions relating flower number (independent variable) to seed set per flower (dependent variable) in Aralia nudicaulis L. in 1984.

Flowering Date	N	Slope	Intercept	r^2	P
June 6	9	0.056	-1.04	0.24	.1829
June 8	6	0.102	-3.21	0.28	.2785
June 10	18	0.053	-0.87	0.24	.0383
June 12	13	0.03	0.34	0.23	.1013
June 14	15	-0.001	2.20	0.00	.9535
All Groups	61	0.036	-0.11	0.21	.0002

Table 24. Summary of linear regressions relating distance to the nearest male flowering ramet (independent variable) to seed set per flower (dependent variable) in Aralia nudicaulis L. in 1984.

Characteristic	N	Slope	Intercept	r^2	P
Flowering Date					
June 6	8	-0.12	2.06	0.099	.448
June 8	5	-0.30	3.16	0.653	.098
June 10	17	-0.02	1.56	0.004	.803
June 12	12	-0.14	2.67	0.195	.151
June 14	14	0.06	1.91	0.027	.576
All Groups	56	-0.07	2.11	0.050	.098
Flower Number					
≤ 41	15	-0.13	2.08	0.244	.061
42-55	19	-0.04	1.48	0.030	.475
≥ 56	16	0.02	2.40	0.008	.741

4.4 Discussion

This study has shown that there is a great deal of variation for secondary sex characteristics in *A. nudicaulis*. Variation in secondary sex characteristics did affect pollination and seed production. A good deal of the variation in seed production is attributed to only two characteristics, flowering time and inflorescence size.

Flowering time was significantly correlated with seed production in both 1983 and 1984 (Table 15, 16), but, the relationship differed between the two years. Seed production was highest at peak flowering in 1983 (Table 15) and was highest in the later stages of flowering in 1984 (Table 16).

The number of flowers per inflorescence was correlated with seed production and the efficiency of seed production, seed set per flower (Table 20, 21, 22, 23). However, the relationship between flower number and seed production also varied within the season in both 1983 and 1984. It is apparent that flowering time and inflorescence size are coupled in their effects on seed production.

The interaction of flowering time and flower number is due partly to the correlation between these two factors. Date of full bloom was negatively correlated with the number of flowers per inflorescence (Table 15, 16). Individual ramets that reached full bloom early in the season were larger but had fewer flowers than individuals that flowered later in the season (Tables 15, 16, 17). If this variation had a heritable component, there could be adaptive tradeoffs

between the advantages of flowering early as suggested by Barrett and Helenurm (1981) and the advantage of a large number of flowers.

The advantage of a large number of flowers may also be counteracted by competition for resources among fruits within an inflorescence. Wyatt (1980) has shown that competition for resources within an umbel is more intense than competition between umbels of an inflorescence. Wyatt (1980) suggested that a compromise between the advantages of a large inflorescence and the problem of competition among flowers within an inflorescence is to reduce the number of flowers per umbel while maintaining umbel number constant. In *A. nudicaulis* female inflorescences have approximately half as many flowers as male inflorescences but the majority of both males and females have three umbels (Fig. 10, Table 14). The main difference in inflorescence size between the sexes is due to females having fewer flowers per umbel. This suggests that the counteracting advantages and disadvantages of a large inflorescence have influenced the present inflorescence size in *A. nudicaulis*. Flowering does appear to be a large drain on resouces, particularly in females, since only 4.8% of females compared to 35.1% of males flowered in consecutive seasons (Table 5).

The degree to which resources or pollination intensity limited reproduction varied between the two years. There was no evidence for pollen limitation of seed set in 1983 (Table 15). In 1984, pollen limited seed set per flower on two

dates during the flowering season (Table 16). Variation in pollinator behavior both within and between seasons affected seed production. Therefore in one season resource limitation and sexual selection may influence the fitness of plant characteristics, while in another season pollen limitation will allow pollinator behavior to influence the fitness of plant characteristics.

The spatial pattern of flowering plants has been shown to influence pollinator movement and seed production in a variety of plant species (Levin 1979, Wyatt and Hellwig 1979, Antonovics and Levin 1980). In the present study there was no significant relationship between distance to the nearest flowering male ramet and seed set per flower (Table 24). The study site was in an area where there was a great deal of intermingling of male and female ramets, therefore pollen transfer was more affected by flowering time and inflorescence size. Barrett and Thomson (1982) found no systematic relationship between fecundity in *A. nudicaulis* and the spatial pattern of male and female flowering ramets in a one hectare forest block. They attributed this to the long flight distances of pollinators and pollen carryover between visits to male ramets.

There was no apparent tradeoff between the number of seeds produced by an individual and seed size (Table 15, 16). Individuals that produced the most seeds had seeds that were as large or larger than seeds of individuals that produced fewer seeds. It is not known whether there is a

tradeoff between seed production and clonal growth. Individuals that had larger inflorescences had smaller ramets (Table 19). This may indicate that there is a tradeoff between allocating resources to sexual reproduction and vegetative growth.

Variation in secondary sex characteristics did affect seed production. However, it is not possible to conclude that a particular characteristic is adaptive because of the variation in effect and the interaction of several characteristics on seed production. Darwin (1859) noted that secondary sex characteristics were often more variable than other characteristics. He suggested that secondary sex characteristics should not be as constant or as uniform as other characteristics because they, "... have been accumulated by sexual selection, which is less rigid in its action than ordinary selection, as it does not entail death but only gives fewer offspring..." (Darwin 1859). Sexual selection is only considered to be possible in plants when female reproductive success is resource limited (Willson 1982). When female reproductive success is pollen limited other factors such as pollinator behavior may affect seed production. Resource limitation and adaptive tradeoffs between temporally varying selection pressures can affect the advantages or disadvantages of various plant characteristics. Variation in the secondary sex characteristics in *A. nudicaulis* should be maintained because of the variation in and the interaction of the

variety of forces acting as selection pressures.

5. Integration

The experiments reported here indicate that mature shoots in *Aralia nudicaulis* are relatively autonomous in their carbon economy. Most carbon exported by a shoot is translocated basipetally into the rhizome section from which a shoot emerged. While the rhizome basipetal to a shoot is a major storage organ, the strongest sinks are actively growing roots and new developing rhizomes adjacent to a shoot.

Several other studies have shown that individual plant modules are autonomous for their carbon economy (reviewed by Newell 1982, Watson and Casper 1984). However, White (1984) has stated that the evidence is ambivalent since physiologists have rarely analysed plants in modular terms. In addition, reciprocal movement of ^{14}C assimilate has been observed between plant parts, particularly in response to disturbance such as defoliation or shading (Ismail and Sagar 1981).

The results of this study indicate that the normal pattern of carbon translocation in *A. nudicaulis* was altered by shading a mature shoot. However, the data were variable and very little carbon was translocated to a mature shaded shoot. The 24 hour translocation period used in this study may have been too short for starch storage reserves in the shaded shoot to be depleted. Experiments using longer translocation times would be necessary to determine if a mature shoot would become a carbohydrate sink.

The changes in translocation pattern after disturbance do indicate that the rhizome system and roots associated with a shaded shoot would be maintained by other connected shoots should the shaded shoot not receive support from adjacent shoots and die. The strong sink strength of new developing rhizome tips adjacent to a shaded shoot also suggests that connected undisturbed shoots would support the development of a new shoot should the shaded shoot not survive. Therefore one of the advantages of shoots remaining physically connected and physiologically integrated is to help local sections of a clone recover from disturbance. Physiological integration may also be a mechanism for increasing the ability of a clone to expand horizontally while each shoot retains the capacity to survive independently if connections are severed (Newell 1982).

It is not possible based on the present results to determine whether the suggestion by Bawa et al. (1982) that physiological integration among shoots may allow for the cost of reproduction to be shared among several shoots within a clone. Studies of the assimilate distribution in clonal plants during flowering would be required to test this hypothesis. However, carbon translocation is only one aspect of the physiological interactions among connected shoots. Reproductive structures can be self-supporting in terms of carbon (Bazzaz et al. 1979), but this is probably achieved at the cost of importing nitrogen from the leaves or other organs (Mooney and Chiariello 1984). Photosynthesis

and carbon gain are generally controlled by the nitrogen content of a photosynthetic structure (Gulmon and Chu 1981, Field and Mooney 1983).

Resource allocation studies have traditionally focused on carbon balance approaches (Watson 1984). The carbon balance approach has been criticized because other resources or developmental constraints may limit plant growth (Watson 1984, Mooney and Chiariello 1984). A multi-resource accounting may be necessary to determine the constraints affecting allocation patterns in plants.

While a great deal of attention has been focused on the patterns of resource allocation, there is little information on what controls the allocation patterns in plants (Mooney and Chiariello 1984). In particular it is not known what controls the allocation changes during the switch from vegetative to reproductive development. Acquisition of sufficient nutrient reserves appears to be one factor controlling the change from vegetative to reproductive development in perennial plants (Jefferies et al. 1979). The nutrient cost of reproduction in females of dioecious plants greatly exceeds the cost of flowering in males (Wallace and Rundel 1979). In *Aralia nudicaulis* this excess nutrient cost in females may be what effects the differences in consecutive flowering pattern between the sexes.

It would be useful to study the allocation patterns of carbon and nitrogen in *Aralia nudicaulis* and other clonal plants before, during and after a shoot flowers.

Fertilization experiments could also be performed to determine the effect of increased nutrient availability on allocation patterns during vegetative and reproductive development.

Inherent in the concept of resource allocation is the idea that different structures or processes are alternatives; a gain in one as a result of selection may be offset by a loss in another (Harper 1977, p. 653). This study illustrated that there was a great deal of variation in secondary sex characteristics in *Aralia nudicaulis* and that many of the characteristics were correlated. Correlations among different sets of characteristics may be the result of different solutions to different selection forces acting on an individual plant at one time. For example, female flowering ramets may be broadly classified into two groups. One group of females has large inflorescences but small shoots and the other group has small inflorescences and large shoots. These two extremes may represent selection for high seed production in one case and increased vegetative growth in the other case. Because of limited resources, selection for one characteristic resulted in tradeoffs in another characteristic.

In addition, individuals with smaller inflorescences reached full bloom earlier than individuals with larger inflorescences. Individuals with smaller inflorescences would be more likely to be affected by competition with males for pollinator service. One method to avoid this

competition would be to flower early as suggested by Barrett and Helenurm (1981).

The evolutionary advantage or disadvantage of a characteristic does depend on the heritability of that characteristic. Since this study was conducted in the field it is not known how much of the observed variation is due to environmental effects. Future studies should attempt to determine if there are genetic differences between ramets with different phenotypic characteristics. Probably the most feasible method to determine the genetic structure of a population of clonal plants like *A. nudicaulis* would be to use electrophoresis techniques.

In addition to the variation observed among ramets, there was variation in the action of selection in the two study years. The variable action of selection would add to the dilemma of adaptive compromises. In years when pollination intensity limits seed production, characteristics which influence pollination success would be selectively advantageous. In other years resource shortages would select for characteristics which influence resource use efficiency and the quality of seeds produced. Variation in characteristics like that observed for *A. nudicaulis* may be maintained because of the variation in selection pressures acting on the population.

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7. Appendix

7.1 Dry weight of plant components

7. Appendix

7.1 Dry weight of plant components (mg, n = 10)

Component	Mean	Standard Deviation	Maximum	Minimum
Leaf	1319.0	840.0	2726.8	166.7
Petiole	166.7	96.5	318.5	61.8
Caudex	1439.3	827.1	2743.4	201.1
Rhizome	5585.1	1489.5	8431.9	3967.9
Roots	1085.1	709.4	2626.2	78.1
New Rhizome Tips	235.6	344.1	1064.4	8.5